THE STRUCTURE AND REACTIONS OF THE TENTACLES OF TEREBELLA MAGNIFICA W.

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Terebella magnifica Webster is a typical sedentary tube worm found under stones in the shallow water of the Bermuda Islands. Like many related forms it possesses numerous tentacular filaments which function in the building of the tube, obtaining food, respiration, and protection. The remarkable feature of these tentacles is their ability to survive and react after removal from the body of the worm. This automaticity and their length, which often exceeds 50 cm. when extended, provides material for numerous physiological experiments. The present paper deals with certain structural aspects of these tentacular filaments and their reactions to light and electrical stimulation.

Specimens of *Terebella* were obtained in large numbers along the shores of Long Bird Island and were easily kept in shallow dishes in running sea water. When gravel was provided they built new tubes and reacted very much as in normal surroundings, except that when exposed to light the tentacles were always more or less contracted, while in nature worms were occasionally seen with their fully extended tentacles exposed to brilliant illumination. The tentacles, which number from 60 to 100 in a large specimen, may extend to a length several times that of the worm or may be tightly coiled in a mass only a few centimeters in length. Tentacles which had been removed from worms survived for twelve days in bowls of sea water provided the water was changed frequently. New tentacles grew at the rate of 1 to 1.5 cm. per day.

Figure 1 is of a section through the midregion of a tentacle. The greatest diameter is about 1 mm. Along one side extends a deep groove. This is lined with ciliated epithelium and the very active cilia beat constantly toward the base of the tentacle. Microscopic examination of a living tentacle shows a constant stream of small particles consisting of diatoms and other small organisms being swept along this groove toward the basal end. The edges of the groove may be tightly applied one to the other, forming a ciliated tube, or they may be applied by a sucking action to rocks and algæ where the food is swept into the tube.

Covering the exposed surface of the tentacle is an epidermis containing numerous mucous glands (Fig. 3), which are more highly specialized than in the earthworm. Upon stimulation with diluted acetic acid, these glands discharge with considerable force, expelling a stream of mucus which forms a filament several times the length of the cell. The discharged gland resembles very closely a discharged nematocyst.

Longitudinal muscle fibers are most numerous, but in addition there is a complicated system of circular, cross, and oblique fibers. This system of muscles enables the tentacle to execute its many movements.

The central portion of the tentacle is a space, possibly continuous with the cœlomic cavity of the worm, containing a fluid in which amœboid cells are numerous.

The nervous system of the tentacle consists of five longitudinal groups of fibers (Fig. 2) with regularly arranged branches. Two large bundles are located one on each side of the tentacle. A medium-sized bundle is found opposite the ciliated groove and between this and the large lateral groups are two smaller bundles. Fibers enter and leave these bundles at regular intervals by way of circular connections which may be seen on one side of the tentacle in Fig. 2 and in a longitudinal section of a tentacle in Fig. 4. These branches may be traced into the region of the ciliated groove, gradually decreasing in diameter as the distance from the longitudinal bundles increases. Because the only material available for histological study was fixed in Bouin's fluid, it was

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Figures 1–6 are photomicrographs taken at various magnifications.

FIG. 1. Cross-section of a tentacle near midregion.

FIG. 2. Detail of region of tentacle containing the longitudinal bundles of nerve fibers and on one side a circular nerve connective which joins these bundles and extends to the side with ciliated groove.

FIG. 3. The mucous glands of the epidermis.

FIG. 4. A longitudinal section through one of the large lateral nerve bundles showing the segmental arrangement of the circular connectives. (This photograph has been retouched in order to accentuate the outlines of the nerve tracts.)

FIG. 5. Details of the region of the lateral longitudinal nerve fiber tracts showing the characteristic thinning of the epidermis over these bundles.

FIG. 6. Some of the nuclei occasionally seen associated with the nerve fiber bundles. These may be nuclei of sensory cells.

CC = circular connective.
LLN = large longitudinal nerve fiber tract.
MN = median nerve fiber tract.
NU = nuclei of nerve or sensory cells.
SLN = small longitudinal nerve fiber tract.


MN
CG
SLN
LLN
1
2
3
LLN
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LLN
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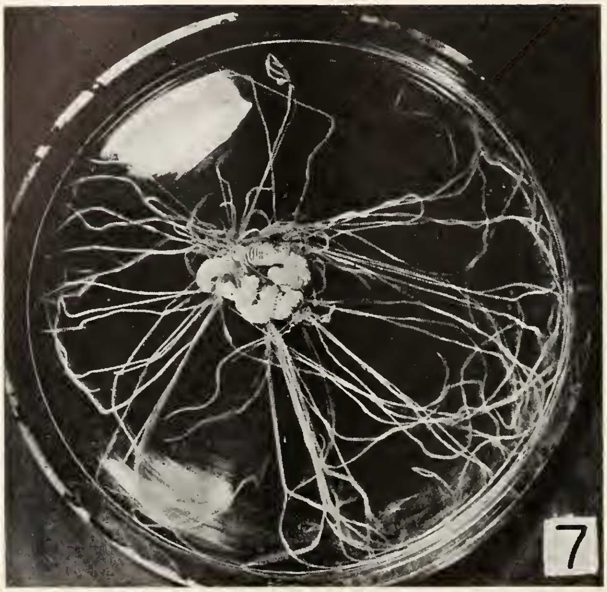

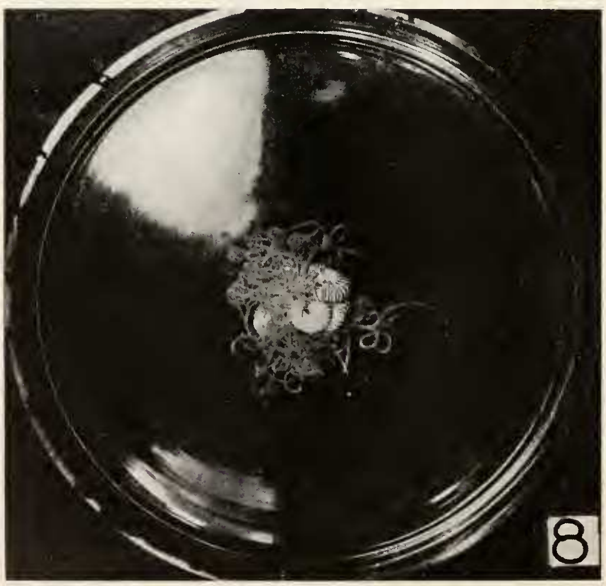

Fig. 7. Photograph of dark-adapted worm taken with a brief flash of light. Note well-extended tentacles.

Fig. 8. Photograph of same worm as seen in Fig. 7 taken few seconds later. Note contracted tentacles.

impossible to trace individual nerve fibers and to locate readily sensory cells. The characteristic thinning of the epidermis over the lateral longitudinal bundles of fibers, seen best in Fig. 5, suggests that the photoreceptors may be located in this region. Nuclei of nerve cells are found in this vicinity and are usually more evident at points where circular connectives join the bundles (Fig. 6). The infrequent occurrence of nuclei within the bundles of nerve fibers leads to the conclusion that few intermediate neurones occur within the tentacle. A study of the responses of isolated and intact tentacles enables one to draw more definite conclusions regarding the functional arrangement of the nervous system of the tentacle.

Reactions of Tentacles to Light

When a specimen of *Terebella* has been in the dark for one-half hour or longer the tentacles are relaxed and extended to full length (Fig. 7). In this condition they are very sensitive to light and illumination with light of a few foot candles in intensity results in a rapid contraction of the tentacles followed by active writhing movements (Fig. 8). The reaction time, even at low intensities of illumination, was found to be too brief to measure accurately with a stop watch but was estimated to average about 0.5 second.

If a tentacle is removed and placed in sea water, in the dark, it behaves as though it were still a part of the animal. It becomes extended and quiescent after a period of dark adaptation and when illuminated reacts in as short a time as does an attached tentacle. The reaction time depends only very slightly on the intensity of illumination and over a range from 5 to 200 foot candles the change could not be measured accurately. It is probable that the use of brief flashes of light as employed by Hecht (1919–1920) in studying the sensitivity of the siphons of *Mya* would have yielded data which might have been studied quantitatively, as the reaction time is doubtless dependent on the length of the exposure period.

When a single attached tentacle is explored with a point source of light, beginning at the base and moving toward the tip, there is seldom a contraction until a portion of the distal third of the tentacle is illuminated. This might be accounted for by assuming a concentration of photoreceptors near the distal end or by assuming a nervous system which conducts primarily toward the base of the tentacle. Further evidence in support of one of these views will appear later.

One other interesting fact regarding the reaction to a point source of light is the independent behavior of single intact tentacles. The illumination of the tip of one tentacle and its subsequent withdrawal is rarely followed by movement of other tentacles. This indicates little coördination between the many tentacles.

Reaction of Tentacles to Electrical Stimulation

In order to obtain further evidence on conduction within the tentacle, electrical stimulation was used. An isolated tentacle was arranged in such a manner that on either side of the electrodes a portion of the tentacle passed over blocks of paraffin. The remainder of the tentacle was in contact with a glass plate where it was kept moistened with sea water. By means of an induction coil both single shocks and repeated stimuli were applied to a midregion of the tentacle. The lowest stimulus which elicited a response of the proximal half of the tentacle never caused a contraction of the distal half. The distal portion contracted only after repeated stimuli of high intensity.

Discussion

The reactions of isolated tentacles of *Terebella* to light and electrical stimulation indicate that there are probably direct connections between receptors and muscles as demonstrated histologically by Dawson (1920), in the ventral region of the earthworm. The experiments of Moore (1923) and Hess (1925), which confirmed Dawson's findings, also lend support to such a view.

The apparently greater sensitivity to light of the distal portion of a tentacle does not mean that the photoreceptors are most abundant in this region. Rand (1909) and Parker (1917) showed that in the tentacles of *Condylactis,* an actinian, conduction over nerves was always proximal. This supported the histological results on *Cerianthus* of Grošelj (1909), who found that almost all of the sensory cells of the tentacles were unipolar, with their fibrils extending without exception toward the base. Such a situation in the tentacles of *Terebella* would account for the apparently greater sensitivity of the distal portion of the tentacle, as a stimulus applied near the tip would have a greater effect on the tentacle, as a whole, than one applied near the base.

That the direction taken by the majority of fibers from receptors is toward the base is evidenced by the response to electrical stimulation. The similarity, in this respect, to the situation in the tentacles of actinians is of considerable interest. The polarity of the tentacle as regards conduction indicates that a nerve plexus or net probably does not exist here. This is in agreement with the recent work of Coonfield (1932) on earthworms.

Summary

1. The tentacular filaments of *Terebella magnifica* W. are remarkably independent in their behavior after removal from the worm. Their functions are varied and they possess many features typical of an intact organism.

2. A deep ciliated groove acts as a collector and conductor of food to the body of the worm. The epidermis contains numerous specialized mucous cells.

3. The nervous system of the tentacle consists of five longitudinal bundles of nerve fibers with circular connectives or branches occurring at regular intervals.

4. Both intact and isolated tentacles are sensitive to light and in either case the reaction time over a fairly wide range of intensities is of the order of 0.5 second.

5. Local electrical stimulation elicits a response of only that portion of the tentacle proximal to the electrodes except when stimulating with rapid shocks of high intensity.

6. The experimental evidence indicates that the nervous system consists of direct receptor-effector elements which conduct primarily toward the base of the tentacle. There was no evidence which would seem to indicate the presence of a nerve plexus or net.

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